Journal of Experimental Marine Biology and Ecology 503 (2018) 129–135

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Seasonally acclimated metabolic Q_{10} of the California horn shark, *Heterodontus francisci*

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ARTICLE INFO

Keywords:
Respirometry
Oxygen consumption
Elasmobranch
Temperature sensitivity
Energetics

ABSTRACT

Dynamic environmental thermal conditions are known to affect physiological processes in ectothermic organisms that may influence movement, distribution and energetic costs. A better understanding of their metabolic Q_{10}, temperature sensitivity, is needed in order to make realistic predictions about how some nearshore populations may respond to changing oceanographic conditions. Oxygen consumption was used as a proxy to measure acclimated standard metabolic rates (SMR) of the California horn shark (*Heterodontus francisci*) at four temperatures (14°, 16°, 20° and 22 °C) typically experienced throughout an annual cycle. Sharks were acclimated in a large holding tank at each of the desired temperatures for at least two weeks prior to the trial. All individuals tested were juveniles, ranging in size from 37 to 48 cm TL and weights of 0.41–0.94 kg. Respirometry trials ranged in length from 6 to 14 h. The estimated (± SE) resting $\dot{M}O_2$ (mg O_2 kg^{-1} h^{-1}) of the CA horn shark at each temperature treatment was 30.6 ± 3.4 (14°, n = 4), 33.9 ± 2.3 (16°, n = 10), 44.9 ± 2.4 (20°; n = 9) and 57.9 ± 2.7 (22 °C; n = 3). The metabolic Q_{10} of the CA horn shark from 14° to 22 °C is 2.01, providing a metric to generate predictive models to estimate minimum metabolic costs associated with changing thermal regimes and global sea temperature rise. Predictions from our model indicate during years 2012 to 2016, rising sea surface temperature associated with a strong El Niño Southern Oscillation (ENSO) event resulted in a 23% increase in minimum metabolic costs for the CA horn shark. The results from our model suggest the CA horn shark may need to adapt compensatory behaviors (e.g., behavioral thermoregulation) to cope with ENSO events and climate change.

1. Introduction

Temperature is a key ecological abiotic factor known to directly affect the rates of physiological processes of marine ectotherms (Brett, 1971; Di Santo, 2016; Di Santo and Bennett, 2011; Fry and Hart, 1948; Hight and Lowe, 2007; Johansen and Jones, 2011; Magnuson et al., 1979; Sibly et al., 2012; Sinclair et al., 2016). While global sea temperature is naturally dynamic, fluctuating between seasons, there is a current, consistent trend of overall increasing global ocean temperature (Boyd and Doney, 2002; Sibly et al., 2012). Because ectotherms are dependent on ambient temperatures and temperature directly affects metabolic rate, a better understanding of their metabolic temperature sensitivity (Q_{10}) is needed to make realistic predictions as to how changing thermal conditions will influence movements, distribution patterns, feeding and growth rates, and reproduction over time (Barnett et al., 2016; Parsons and Carlson, 1998; Sinclair et al., 2016). Temperature sensitivity in metabolism is quantified by calculating an organism's Q_{10}, the degree to which metabolism changes over a 10 °C change in temperature (Gillooly et al., 2001; Schmidt-Nielsen, 1997). Because there are additional costs associated with physiological temperature acclimation (Angilletta, 2009), to acquire an accurate measure of acclimated metabolic Q_{10} requires animals to be slowly acclimated to treatment temperature prior to measurement. Non-acclimated measurements of temperature sensitivity have been shown to potentially overestimate metabolic Q_{10} (Bernal and Lowe, 2015; Carlson and Parsons, 1999). Most respirometry studies previously conducted on elasmobranchs have been on non-acclimated animals (e.g., experiencing fluctuations in temperature throughout respirometry trials) (Di Santo and Bennett, 2011; Hopkins and Cech, 1994; Miklos et al., 2003; Neer et al., 2006).

Oxygen consumption rates of ectothermic elasmobranchs have been used as a proxy for metabolic rates, and thus the current physiological state of the organism (Hopkins and Cech, 1994; Lowe, 2001; Miklos et al., 2003). Coastal elasmobranch species, most of which are ectothermic, are important top and meso-level predators in marine ecosystems. For example, Cortés (1999) estimated that out of 149 coastal

Abbreviations: SMR, standard metabolic rate; ENSO, El Niño Southern Oscillation; $\dot{M}O_2$, mass specific oxygen consumption rate (mg O_2 kg^{-1} h^{-1})

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https://doi.org/10.1016/j.jembe.2018.02.006
Received 1 October 2017; Received in revised form 16 February 2018; Accepted 21 February 2018
Available online 27 March 2018
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and pelagic shark species, trophic levels ranged from secondary to tertiary consumers (Trophic Level 3.1–4.7), subsequently impacting lower trophic levels through top-down processes. Therefore, determining the degree of temperature sensitivity in these species is important to be able to forecast how changing ocean temperatures may affect their behavior, and could thus have potential cascading trophic effects on these thermally dynamic ecosystems (Cortés, 1999; Ferretti et al., 2010).

This study used the California horn shark (CA horn shark; *Heterodontus francisci*) as a model species due to their importance as a meso-predator (trophic level = 3.2; Cortés, 1999) in the kelp forest ecosystem (Strong, 1990). In addition, they have a comparatively small size range (maximum TL ≤ 122 cm) and their non-obligate ram ventilation ability allows for them to exhibit long periods of inactivity making it relatively easy to quantify their minimum energetic costs (Compagno, 2001). The CA horn shark is an ectothermic, demersal, reef-associated shark that commonly uses shallow habitats (2–11 m), but may venture into deeper habitat for short periods of time (Compagno, 2001). They are found from central California to the Gulf of California (Compagno, 2001; Love, 1991), and are an important food fish in Mexican elasmobranch fisheries (Ramirez-Amaro et al., 2013). This species is currently listed as data deficient on the IUCN Red List (Carlisle, 2015), and because they are a known sea urchin predator, similar to the California sheephead (*Semicossyphus pulcher*), they may also serve as an important keystone predator in the kelp forest ecosystem as sea urchins can over graze a kelp forest if densities become too high (Compagno, 2001; Cowen, 1983; Strong, 1990; Tegner and Levin, 1983).

It is important to understand how physiologically-sensitive the CA horn shark is to temperature change in order to make realistic predictions as to how increasing ocean temperatures as well as major oceanographic events (e.g., El Niño Southern Oscillation) may affect the daily behavior (e.g., resting, foraging, mating and distribution) of these sharks. Temperate regions such as the northeast Pacific are subject to El Niño Southern Oscillation (ENSO) events, which cause a reduction in upwelling and a concurrent increase in sea surface temperatures (SST) (Tegner and Dayton, 1987). Commonly residing in shallow demersal habitats most affected by ENSO events, it is important to understand how these thermally dynamic events may alter the metabolic rates and thus the behavioral ecology of the CA horn shark. Because CA horn sharks are thought to be annual residents to southern California reefs, and are exposed to a large annual temperature range, it is hypothesized that this species should exhibit a low temperature sensitivity (≤ 2) (Strong, 1990). The goal of this study was to measure the acclimated metabolic Q_{10} of the CA horn shark across a range of seasonal water temperatures, and to model the effects of multiple ENSO events and increasing ocean temperatures on their minimum energetic costs.

2. Methods

2.1. Capture and maintenance

Sharks were collected by hand via scuba along the coast of southern California and Santa Catalina Island and were transported back to the laboratory in large aerated coolers with frequent water changes. All sharks were maintained in a 2070 L holding tank at the California State University Long Beach (CSULB) Shark Lab and were fed a diet of shrimp and squid three times a week until satiation. Water temperature of the holding tank was controlled using a Cyclone coiled chiller or a Finnex titanium heater at ± 0.5 °C of the desired temperature.

2.2. Acclimation

Sharks in this study were acclimated to each treatment temperature (14° (n = 4), 16° (n = 10), 20° (n = 9) and 22 °C (n = 3)) for at least two weeks prior to each trial (Table 1) (Rummer et al., 2014; Whitney et al., 2016). This was done to reduce the additional costs associated with physiological acclimation (Angilletta, 2009). While it was previously thought longer acclimation periods lead to lower (and less accurate) measurements of metabolic sensitivity (Burggren and Roberts, 1991; Carlson and Parsons, 1999; Neer et al., 2006; Schmidt-Nielsen, 1997), it has since been shown that adequate acclimation is necessary to not overestimate the metabolic rate, especially when working at water temperatures close to seasonal extremes (Bernal and Lowe, 2015; Chabot et al., 2016; Clarke and Fraser, 2004; Rummer et al., 2014). Temperature of the holding tank was adjusted in increments of 1 °C per day until the desired temperature was reached. Not all sharks were tested in the same order, or acclimated for the same duration of time (Table 1). The addition of two extra treatment temperatures (14° and 22 °C) were added towards the end of the study, which resulted in lower sample sizes at those temperatures.

2.3. Respirometry

To measure oxygen consumption rates of the sharks, a 90 L Loligo Brett-style swim tunnel respirometer housed at the CSULB Shark Lab was used to conduct closed respirometry (Steffensen, 1989; Svendsen et al., 2016). Individual sharks were fasted for 48 h prior to trial to eliminate any costs associated with specific dynamic action (SDA) (Chabot et al., 2016; Dowd et al., 2006; Du Preez et al., 1988). Sharks were placed in the respirometer at least 12 h prior to the start of the trial to allow for acclimation to the working chamber and an opaque sheet was placed over the chamber to reduce disturbance during the trial (Chabot et al., 2016; Du Preez et al., 1988; Neer et al., 2006; Whitney et al., 2016). Because this study aimed to determine standard (resting) metabolic rate (SMR) of the CA horn shark, water velocity inside the working chamber was kept at 0.13 m/s only to maintain a directed flow of water over the shark, preventing stratification (Steffensen, 1989), but not strong enough to induce swimming. All sharks remained resting on the bottom of the respirometer for the duration of the trial. All trials were conducted during daylight hours when these sharks are normally resting, and visual observations of the shark throughout the duration of the trial indicated movement < 5% of the time; therefore, we are confident that oxygen consumption measures are representative of true SMR (Chabot et al., 2016). A PSt3 fiber optic oxygen sensor (± 0.05 mg/L) and PT 1000 temperature sensor (± 0.5 °C) were used to measure and record dissolved oxygen (DO_2) and water temperature in the working chamber using Oxyview Precision Sensing software. Because there was a relatively high ratio of respirometer to shark volume (95–220:1), trials were run until DO_2 reached 80% saturation (Steffensen, 1989; Svendsen et al., 2016; Whitney et al., 2016). Each trial consisted of at least two oxygen consumption-resaturation events with a 15 min flush occurring after each segment to bring DO_2 levels back to ~100% saturation. Trials ranged from 6 h at 22 °C to 14 h at 14 °C, and only the second segment from each trial were used for analysis. At the end of each trial, the shark was removed from the respirometer and a one-hour blank measurement was recorded to obtain background respiration (Graham et al., 1990; Lowe, 2001). Upon removal from the respirometer sharks were weighed to the nearest kilogram and their volume was measured to the nearest 1 mL.

2.4. Data analysis

Linear regression was used to determine the rate of oxygen consumed during the second measurement of each trial, $r^2 > 0.99$ for all trials (n = 26). We then calculated the adjusted oxygen consumption rate (R = mg O_2 L^{-1} s^{-1}) of each shark using the eq. R = T-B (Graham et al., 1990). Where T (mg O_2 L^{-1} s^{-1}) represents the rate of oxygen consumed during a segment and B (mg O_2 L^{-1} s^{-1}) represents the rate of oxygen consumed during the blank. Using this adjusted oxygen consumption rate (R) we calculated the mass specific oxygen consumption rate by each shark (Steffensen, 1989):

Table 1
Acclimation durations and testing sequence at respective treatment temperatures for all CA horn sharks in this study. Trials were run from January 2015 to November 2016, acclimation time and order varied among sharks. Note that not all sharks were tested at all four temperature treatments.

Shark ID	Acclimation duration prior to treatment temperatures				Order tested at treatment temperatures			
	14 °C	16 °C	20 °C	22 °C	14 °C	16 °C	20 °C	22 °C
1	2 wk	3 wk	4 wk	2 wk	3	2	1	4
2	2 wk	11 wk	7 wk	3 wk	3	2	1	4
3	–	8 wk	6 wk	–	–	1	2	–
4	–	4 wk	2 wk	–	–	1	2	–
5	–	10 wk	8 wk	–	–	2	1	–
6	–	3 wk	10 wk	–	–	2	1	–
7	–	3 wk	11 wk	–	–	2	1	–
8	–	3 wk	11 wk	–	–	2	1	–
9	2 wk	4 wk	3 wk	2 wk	1	2	3	4
10	2 wk	4 wk	–	–	1	2	–	–

$$\dot{M}O_2 = \frac{R \bullet 3600\ s \bullet (V - D)}{W}$$

where $\dot{M}O_2$ (mg O_2 kg^{-1} h^{-1}) is mass specific oxygen consumption, R is the adjusted rate of oxygen consumption, V is the volume of the respirometer (90 L), D is the displacement volume of the shark (L) and W is the wet weight of the shark (kg). Since oxygen consumption is correlated with body size, and body masses of sharks used in this study ranged from 0.41 to 0.94 kg, $\dot{M}O_2$ values calculated here were corrected for body size to a 0.6 kg animal (mean size of sharks in this study) using a scaling exponent of 0.8 (Brett and Groves, 1979). A repeated measures analysis of variance (RM ANOVA) was used to determine the effects of acclimation time on $\dot{M}O_2$, where temperature was the within subject factor.

Due to an unequal sample size across temperatures, a Linear Mixed Effects model (LME; using the lmer function from the *lme4* package in R (Bates et al., 2015)) was used to yield an estimate of $\dot{M}O_2$ at each temperature treatment, and to account for the repeated measures of individuals tested at multiple temperatures. Temperature was treated as a fixed factor and individual was treated as a random effect. The model assumed a normal distribution among all temperature treatments. Additionally, we used a Shapiro-Wilk normality test and found there was a normal distribution among $\dot{M}O_2$ values at each temperature treatment ($p > 0.1$). To test the significance of our LME we compared it to a null model, which assumed temperature had no effect on $\dot{M}O_2$ using Akaike's Information Criterion (AIC) to compare the models.

Q_{10} was calculated two different ways, first using the traditional equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10°C}{T_2 - T_1}}$$

where R_1 and R_2 are the known metabolic rates at their respective temperatures, T_1 and T_2 (°C) (Schmidt-Nielsen, 1997). The $\dot{M}O_2$ estimates from the LME were used to calculate Q_{10} between three selected temperature ranges, 14° to 16°, 16° to 20°, 20° to 22 °C, as well as the entire temperature range of the study14° to 22 °C. However, due to the limitations of the traditional Q_{10} equation (e.g., having more than two temperatures and corresponding metabolic rates), we also used a Nonlinear Regression model (NLR; using the Q_{10} function from the *respirometry* package in R (Birk, 2017)) to generate a Q_{10} value using all data points. All statistical analyses and figures were completed using R (Version 3.2.2) (R Core Team, 2016).

2.5. Model development

Historic, locally relevant SST data were obtained and used to model seasonal and inter-annual changes in minimum metabolic costs for a 0.6 kg CA horn shark based on the temperature sensitivity measured in this study. To make predictions as to how increasing water temperature may affect minimum resting energetic costs, we developed a model to predict these costs spanning several ENSO events. Because CA horn sharks often use demersal habitats within the upper mixed layer of the water column (Love, 1991), and for the purpose of estimating minimum energetic costs spanning several ENSO events, we used daily sea surface temperature (SST) averages over a 12-year period (2004 to 2016) from the National Oceanic and Atmospheric Association (NOAA) Buoy 46,222 located in the San Pedro Channel (33.618 N, 118.317 W) (ndbc.noaa.gov). To convert $\dot{M}O_2$ to SMR in kilojoules (kJ kg^{-1} d^{-1}) we used the oxy-calorific coefficient of 13.6 (J mg^{-1} O_2 consumed) to convert O_2 consumption rate into heat production for a ureotelic organism (Brett and Blackburn, 1978; Brett and Groves, 1979; Elliott and Davison, 1975; Lowe, 2002). Using the equation from the NLR to calculate Q_{10}, we calculated the predicted SMR for a 0.6 kg CA horn shark at each daily average SST recorded:

$$SMR = 3.69 \bullet e^{0.06959 * SST}$$

3. Results

3.1. Respirometry

The estimated $\dot{M}O_2$ (± SE) from the LME at each temperature treatment was 30.6 ± 3.4 (14°, $n = 4$), 33.9 ± 2.3 (16°, $n = 10$), 44.9 ± 2.4 (20°; $n = 9$) and 57.9 ± 2.7 (22 °C; $n = 3$) (Table 2, Fig. 1). $\dot{M}O_2$ ranged widely among individuals across temperature treatments: 25.4–43.2 (14°), 21.4–53.8 (16°), 27.8–59.7 (20°) and 53.8–60.5 (22 °C). $\dot{M}O_2$ was not affected by acclimation time for all temperature treatments (RM ANOVA, $F_{(1,\ 21)} = 2.593$, $p > 0.1$). The LME had a lower AIC value than the null model, indicating a better fit of the data ($X^2 = 34.21$, df = 3, $p < 0.001$). Using the traditional equation, the following metabolic Q_{10}'s were calculated for the CA horn shark: 1.66 (14° and 16 °C), 2.03 (16° and 20 °C), 3.55 (20° and 22 °C) and 2.22 (14° to 22 °C). The NLR resulted in a Q_{10} of 2.01 from 14° to 22 °C for a 0.6 kg CA horn shark (Fig. 1).

3.2. Model outcomes

SMR (kJ kg^{-1} d^{-1}) was modeled for a 0.6 kg CA horn shark at each daily average temperature from 2004 to 2016 (Fig. 2). Two linear models were used to compare the relationship between SST and time for two different time periods within the model. The first from September 2004 to December 2011 ($y = -1.8 \times 10^{-9}\ x + 14.4$) and the second from January 2012 to December 2016 ($y = 1.7 \times 10^{-8}\ x - 11$), with the break occurring at the inflection point (Fig. 2). The model indicated during the period from 2012 to 2016, mean minimum metabolic costs for a 0.6 kg shark increased 23%, compared to the period between 2004 and 2011 where costs decreased by 3.4%. When comparing the change in mean minimum metabolic costs from previous ENSO events in 2006

Table 2
Summary statistics for all CA horn sharks tested in this study. Trials were run from January 2015 to November 2016 and mass, volume and TL of each shark is reported for the duration of time they were tested. Standard metabolic rate (SMR; mg O_2 kg^{-1} h^{-1}) totals for all sharks are fixed effect estimates from a linear mixed effects model (± SE). Note that not all sharks were tested at all four temperature treatments. Additionally, a scaling coefficient of 0.8 was used to correct SMR values to a body size of 0.6 kg (Brett and Groves, 1979).

Shark ID	Mass range (kg)	Volume range (L)	TL range (cm)	SMR (mg O_2 kg^{-1} h^{-1}) at corresponding treatment temperatures			
				14 °C	16 °C	20 °C	22 °C
1	0.56–0.88	0.55–0.85	42–43	30.0	26.1	47.3	55.4
2	0.44–0.62	0.40–0.60	37–38	25.4	24.7	38.1	53.8
3	0.50–0.53	0.49–0.51	41	–	33.8	48.4	–
4	0.41–0.44	0.38–0.41	37	–	35.0	39.5	–
5	0.45–0.51	0.42–0.52	37.5	–	21.4	40.8	–
6	0.63–0.68	0.61–0.63	43	–	53.8	59.7	–
7	0.48	0.43–0.44	39.5	–	23.7	27.8	–
8	0.58–0.63	0.65–0.72	45	–	30.1	39.2	–
9	0.78–0.94	0.81–0.90	45–48	32.9	40.7	50.3	60.5
10	0.76–0.80	0.75–0.78	48	43.2	49.6	–	–
Mean ± S.E.	0.41–0.94	0.38–0.90	37–48	30.6 ± 3.4	33.9 ± 2.3	44.9 ± 2.4	57.9 ± 2.7

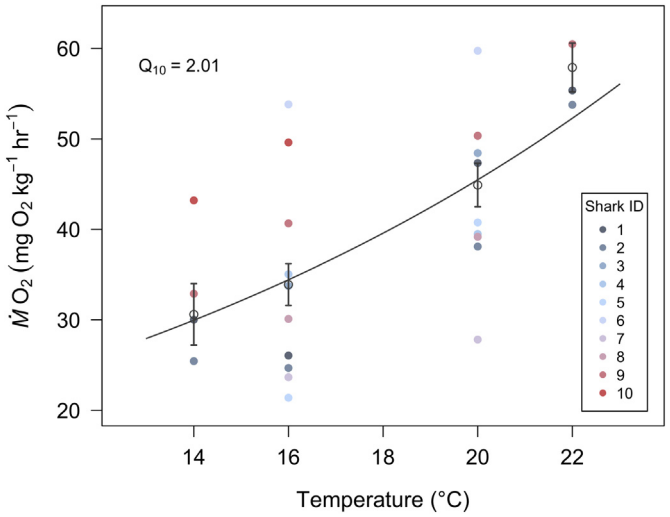

Fig. 1. $\dot{M}O_2$ (mg O_2 kg^{-1} h^{-1}) of the CA horn shark at four temperature treatments. Data from individual sharks at 14 °C (n = 4), 16 °C (n = 10), 20 °C (n = 9) and 22 °C (n = 3) are plotted in unique color to match each shark ID. The estimates from a linear mixed effects model are plotted in open black circles (± SE). The Q_{10} reported is the result of the nonlinear regression ($y = 11.309e^{0.06959x}$).

(temperature range 8–21 °C) and 2009 (8–19 °C) to the most recent event in 2015 (10–21 °C), there was a 12% increase in metabolic costs between those events.

4. Discussion

While there was an expected significant increase in oxygen consumption with increasing body mass (Gillooly et al., 2001) and temperature (Clarke and Fraser, 2004), we did not see any asymptote or drop in $\dot{M}O_2$ at the highest temperature treatment indicating individuals were not reaching an upper thermal tolerance limit (Neer et al., 2006). We saw a high degree of variability in $\dot{M}O_2$ among individuals, which has been observed in other species (Lowe, 2001; Whitney et al., 2016). The greatest variability in $\dot{M}O_2$ was seen among sharks at 16° and 20 °C temperature treatments where sample sizes were highest. It is possible some of the variability in $\dot{M}O_2$ among individuals was attributed to differences in longer duration of temperature acclimation (Table 1); however, there was no significant difference among $\dot{M}O_2$ values at each treatment temperature with respect to acclimation length. There is little known about the speed of temperature acclimation among and within species (Rummer et al., 2014); therefore, it is possible that two weeks may be insufficient for full temperature acclimation and may still result in slightly higher costs. Some studies have indicated that individual variability may be explained by different tissue-specific mitochondrial efficiencies (Clarke and Fraser, 2004; Salin et al., 2016). Salin et al. (2016) examined the mitochondrial properties in the liver and white muscle tissue of juvenile brown trout (*Salmo trutta*) and found that organisms with higher SMR's have mitochondria in the liver with more protons that leak energy (ATP), suggesting lower efficiency and a need for higher SMR to compensate.

While the accuracy of the traditional Q_{10} equation has been questioned before (Gillooly et al., 2001), using the NLR to calculate Q_{10} may provide a more accurate approach. We expected the metabolic Q_{10} of the CA horn shark to be low (≤2) due to their behavior and ecology, and we found this to be true (Fig. 1) (Clarke and Fraser, 2004). Because CA horn sharks are a demersal, non-obligate ram ventilator, and appear to be a non-migratory species, we believe an overall Q_{10} of 2.01 is an accurate representation of their temperature sensitivity. Interestingly, the CA horn shark exhibited a remarkably high metabolic Q_{10} (3.55) between 20° and 22 °C, more than doubling their Q_{10} (1.66) between the lowest temperature treatments of 14° and 16 °C. This higher metabolic Q_{10} at warmer temperatures may suggest that the CA horn shark physiologically performs better in cooler conditions and likely exhibits some compensatory behaviors, such as behavioral thermoregulation when conditions become more energetically costly (Hopkins and Cech, 1994). Behavioral thermoregulation in the form of shuttling between different heterogeneous environments to optimize energy gain and minimize metabolic expenses has been observed in other ectothermic elasmobranch species (Hight and Lowe, 2007; Matern et al., 2000; Papastamatiou et al., 2015; Sims et al., 2006). For example, the lesser spotted dogfish (*Scyliorhinus canicula*), a demersal elasmobranch species, exhibit a strategy known as “hunt warm, rest cool”, whereby warmer habitats above the thermocline is used for foraging, and cooler habitats below the thermocline were used for resting in an attempt to slow digestion and increase nutrient assimilation (Sims et al., 2006). It is presumed this form of behavioral thermoregulation lowered net energetic costs for the dogfish by ~4% (Sims et al., 2006). The CA horn shark could utilize this behavior during ENSO events to move to deeper, cooler water in an attempt to slow their metabolism and reduce energetic costs. While this species is primarily found in shallow habitats, they have been observed as deep as 150 m (Compagno, 2001). Additionally, an ecomorph congener of the CA horn shark, the Port Jackson shark (*Heterodontus portusjacksoni*), has been shown to make long-range seasonal migrations (100 s of km) between foraging and mating habitats (McLaughlin and O'Gower, 1971; O'Gower, 1995; Powter and Gladstone, 2009), showing the potential for the CA horn shark to make long distance movements if needed.

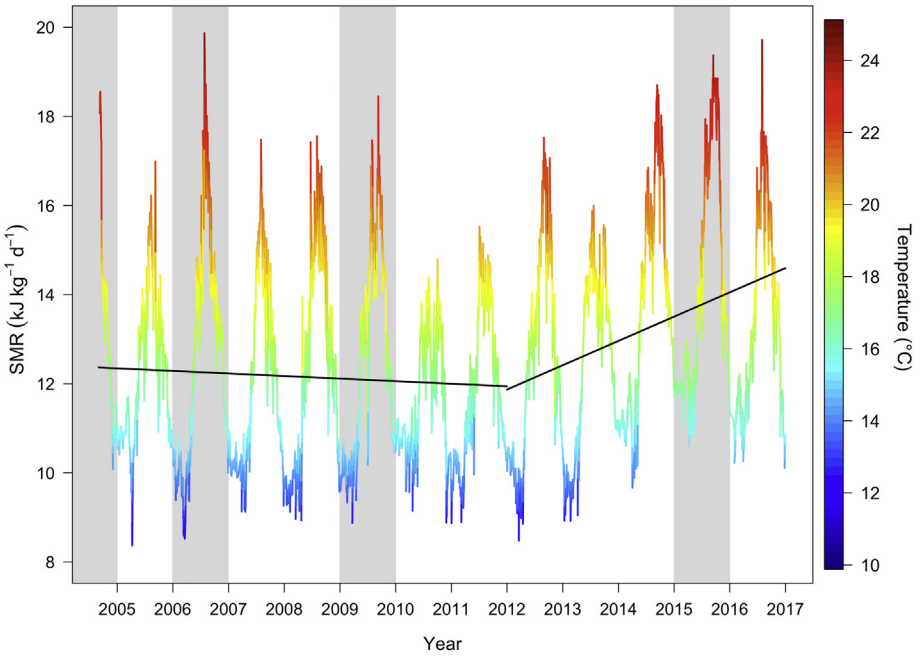

Fig. 2. Predicted standard metabolic rate (SMR) of the CA horn shark from 2004 to 2016. SMR was calculated using data in this study and sea surface temperature (SST) data from National Oceanic and Atmospheric Association buoy data. Metabolic rates were calculated for each temperature using the equation of the line from a linear mixed-effects model exhibiting the relationship between SMR and temperature. The shaded grey areas indicate El Niño periods and the black regression lines represent mean metabolic costs from 2004 to 2011 ($y = -1.8 \times 10^{-9}\ x + 14.4$) and 2012 to 2016 ($y = 1.7 \times 10^{-8}\ x - 11$).

The model presented here (Fig. 2) illustrates a high degree of inter-annual variation, with the warmest and coolest values steadily increasing from 2012 to 2016. The model also illustrates an inter-annual increase in the duration of time where water temperature is warmer and thus minimum metabolic costs are higher. When comparing annual SST during the ENSO events in 2006 and 2009 to 2015, there was a 96.9% increase in the proportion of time SST was at or above 20 °C. In 2015 alone, 35% of the year SST was at or above 20 °C, when CA horn shark metabolic rates and sensitivity are highest. As the proportion of time these sharks spend in warmer water continues to rise, minimum energetic demands increase as well, which could result in increased foraging efforts or shifts to deeper, colder waters where prey abundance may be lower. During ENSO events, some important prey species (e.g., urchins, squid, crustaceans) of the CA horn shark are negatively affected as well (Compagno, 2001; Cortés, 1999; Strong, 1990). For example, the California market squid (*Loligo opalescens*) experience smaller over all body sizes (sometimes half their normal size) as a result of slower growth rates due to lower productivity from the warmer ocean temperatures (Jackson and Domeier, 2003). Additionally, with a decrease in giant kelp (*Macrocystis pyrifera*) coverage due to increased ocean temperatures, we may also see a decrease in urchin abundance due to their increased need to forage outside of their protective crevices, making them more susceptible to predation (North and Zimmerman, 1984; Schiel and Foster, 2015; Tegner and Dayton, 1987). This could force sharks to switch to less nutritional prey or behavioral shifts in habitat use with the absence of some prey species (e.g., urchins, squid) due to ENSO events and climate change. Prolonged periods of strong ENSO events could result in decreased growth for the CA horn shark, which may induce behavioral thermoregulation (e.g., shuttling) or migration to more suitable reefs in deeper water. Similarly, some fish species in temperate regions (e.g., salmon (*Oncorhynchus* spp.), skipjack tuna (*Katsuwonus pelamis*), horse mackerel (*Trachurus trachurus*)) have been known to exhibit spatial and distributional shifts with warmer temperatures (Roessig et al., 2004). Because the CA horn shark's temperature sensitivity increases at higher temperatures, fitness may be increased during La Niña occurrences or cooler years, where costs are lower and prey may be more abundant due to greater kelp productivity in cool water (North and Zimmerman, 1984; Tegner and Dayton, 1987). More detailed dietary studies during ENSO and La Niña events could help shed light on how this species responds to changing ocean conditions.

Not only does our model demonstrate the large amount of annual variability in the CA horn shark's SMR, it also indicates a high degree of seasonal variability as well. While there was little annual variation from 2005 to 2012, apart from the two ENSO events occurring in 2006 and 2009, there are considerable intra-annual differences among these years. During 2006, there was an 80% difference between the seasonal range of daily SMR values from the high peak (summer/fall) to the low peak (winter/spring) in that year. Similarly, in 2009 there was a 70% difference in seasonal minimum metabolic costs. To compare these findings to the most recent ENSO event that occurred in 2015, we estimate there could have been a 58% difference in the seasonal range of metabolic rates. The intra-annual range of these values is showing a consistent decreasing trend, resulting in less predicted fluctuation in SMR, and higher overall values in most recent years.

Using SST as a proxy for shallow demersal depths (2–11 m) where the CA horn shark is commonly found most likely has resulted in an overestimation of minimum energetic costs in regards to temperature, since sharks may be moving between thermal habitats to reduce costs. While minimum energetic costs only provide a baseline, sharks are obviously accruing costs associated with movement and digestion; nonetheless, this simple model provides a framework to make annual predictions of CA horn shark behavior and distribution.

In comparison with other species of elasmobranchs, the CA horn shark has a low overall metabolic Q_{10} (2.01), which was expected given it experiences large seasonal temperature fluctuations annually. Non-migratory species that experience large fluctuations in temperature may have lower overall metabolic Q_{10}'s; but compensate for fluctuating prey availability through behavioral adaptations. Similar to the CA horn shark, the lesser spotted dogfish also has a low to moderate metabolic Q_{10} (2.20, 7°–17 °C; Butler and Taylor, 1975), and is another coastal, residential species only making diel vertical migrations as a form of behavioral thermoregulation (Butler and Taylor, 1975; Sims et al., 2006). The nurse shark (*Ginglymostoma cirratum*), which lives a similar demersal, sedentary lifestyle to the CA horn shark has a slightly higher metabolic Q_{10} (2.42, 23°–30 °C; Whitney et al., 2016), which could be attributed to this species making partial seasonal migrations between Florida and the Dry Tortugas Islands (Pratt et al., 2018). It is important to note many elasmobranch species with reported Q_{10}'s were not acclimated to treatment temperatures prior to being tested and some

experienced temperature changes throughout the duration of the experiment, which can make direct comparisons difficult. For example, the bat ray (*Myliobatis Californica*, Q_{10} = 3.00, 8°–26 °C; Hopkins and Cech, 1994) and the leopard shark (*Triakis semifasciata*, Q_{10} = 2.51, 10°–26 °C; Miklos et al., 2003) experienced 0.5 °C per hour changes in temperature while transitioning between treatment temperatures, and were only allotted 12 h for acclimation once at the desired temperature. These factors may represent potential overestimations of metabolic rates due to lack of sufficient physiological acclimation and cellular inefficiencies (Bernal and Lowe, 2015; Carlson and Parsons, 1999). Duration of physiological acclimation is an important factor that needs to be taken into account when attempting to measure metabolic costs (Bernal and Lowe, 2015).

This study has provided a baseline for the minimum metabolic costs of juvenile (0.6 kg) CA horn sharks across a range of current seasonal temperatures. Using these data, we can begin to model potential movements and interspecific competition of the CA horn shark, which may provide insight into future species distribution. Simple bioenergetics models offer a framework to quantify how other variables influence costs. Higher resolution thermal maps as well as inter-annual monitoring of CA horn shark prey species could improve model predictions and potentially help indicate tipping points for CA horn shark populations. Fine-scale behavior and movement data of the CA horn shark through different thermal regimes would also be beneficial in supporting these data. If warming ocean conditions continue there could be negative effects on CA horn shark populations due to increased metabolic costs, subsequently resulting in adverse effects on kelp bed communities with a lower abundance of an important urchin predator. Based on this current climate trend, we may expect to see a shift in the distribution of the CA horn shark into deeper, cooler waters, migration or distribution of these sharks further north, or potentially physiological adaptations to these warming conditions.

Acknowledgements

We would like to thank California State University, Long Beach for acquisition and use of the swim tunnel respirometer. This work was also supported by the SCTC Marine Biology Foundation, the Los Angeles Rod and Reel Club and the California State University Council on Ocean Affairs, Science and Technology (COAST). We would also like to thank Ryan Logan and Connor White for assistance with data analyses and revisions of this manuscript. Finally, we thank Emily Meese, Racine Rangel, Armand Barilotti and Jillian Sawyna for help with animal collections, as well as Yvette Ralph for help with animal husbandry and technical support.

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